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GENETIC DIVERSITY OF LITTER SIZE TRAITS BETWEEN PARITIES IN RABBITS

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Abstract

Data from two selection experiments for litter size at weaning has been analysed using an univariate pseudoexpectation approach to estimate variance components, fixed effects (reproductive state of the doe and year season effects) and genetic and environmental trends.

The aim of this paper was to check the model commonly assumed for litter size traits, that litter size records of different parities are repeated measures of the same trait. Equal heritabilities and genetic correlation of one are the assumptions of this model.

The analysis involved 8 and 11 generations of selection, 2084 and 2624 litters, respectively, for each experiment.

The traits analysed were litter size at birth, at weaning (28 days) and at 77 days.

The results revealed important differences in prolificacy between both lines (≈2 rabbits) and differences in the heretabilities of litter size of different parities. The heritability of first parity litter size ranged from 0.1-0.14. Evidences has been obtained of lower heritabilities of second and third parities litter size in the most prolific line, especially for the third parity. These differences, if they exist, seem less important in the less prolific line. There were, also, suggestions of genetic correlations of less than one between litter sizes in both lines. The implication of these results on selection for litter size is discussed.

Introduction

Litter size at birth, weaning or slaugther time is important in meat production of rabbits or pigs. It has been the selection objective of several experiments (Ollivier & Bolet, 1981; Rochambeau, 1988; Estany *et al*, 1989; Rouvier, 1991) and the genetic response, when estimated, has been lower than expected.

Low intensities of selection (Ollivier & Bolet, 1981;Estany et *al*, 1989), maternal effects opposite to direct genetic effects (Haley *et al*, 1988), genetic correlations between parities less than one (Bolet & Legault, 1982; Le Roy *el al*, 1987) or imbreeding (Rouvier, 1991) have been advanced as explanations for poor responses.

High selection intensities applied to select hyperprolific females seem promising in pigs (Bichard & David, 1985). Some theoretical studies (Van der Steen, 1985) show that maternal effects lowering genetic response in the long term, are not important. HALEY *et al* (1988) summarise estimates of heritabilities of litter size in pigs and genetic correlations between parities concluding that the heritability of litter size is around 0.1, that there are not significant differences between heritabilities within parities and that there is no strong evidence for genetic correlations substantially lower than one between parities.

The aim of this paper is to analyse two selection experiments for litter size in rabbits in order to check if the results support or not the assumptions of the experiments: that litter size at different parities are repeated records of the same trait.

Material and Methods

Two lines, A (New Zealand White) and V (synthetic line) were used in the experiment. They were selected on litter size at weaning (28 days of age). The selection method for line A was a family index including records of litter size at weaning of the doe to be evaluated, her mother and her full and half sisters (Baselga *et al*, 1984). The method used for line V was a BLUP, being the underlying mixed model as follows:

$$Y_{ijkl} = L_i + E_j + a_k + p_k + e_{ijkl}$$

where,

Li, is the reproductive state of the doe at mating (fixed). There are three levels, nulliparous, N (i=1), lactanting doe, L (i=2) and non nulliparous non lactanting doe, NL (i=3).

E_j, is the year-season in which the parity was made (fixed). There are 33 year seasons for line A and 23 for line V (Table I).

a_k, is the additive value of the doe (random)

p_k, is the permanent non genetic effect on all the parities of the doe (random).

e_{ijkl}, is the temporary environmental effect on the l^{th} parity of the k^{th} doe.

Y_{ijkl}, is the litter size at weaning of the l^{th} parity of the k^{th} doe made in the j^{th} year-season and i^{th} reproductive state of the doe.

The parameters used for the family index and BLUP were h^2= 0.13 and r= 0.20 (García *et al*, 1982).

Tables I and II give information about the size, duration and other aspects of the selection experiments.

TABLE I - ORIGIN, NUMBER OF YEAR SEASON (YS), GENERATIONS (GEN), MALES(NM) AND FEMALES (NF) AND SELECCION METHOD

LINE	ORIGIN	YS	GEN	NM	NF	SELECTION METHOD
A	Newzealand white	33	11	171	1241	family index
V	synthetic	23	8	125	957	BLUP

TABLE II - NUMBER OF PARTURITIONS BY PARITY ORDER

LINE	1st	2nd	3rd	After 3rd
A	1091	552	474	267
V	951	729	559	385

The analysis of the selection experiments has been approached by univariate mixed model methods and carried out separately for the following traits and data sets:

- litter size at birth (number of born alive), NB
- litter size at weaning, NW
- litter size at 77 days, NS

+ first parity data (1)
+ second parity data (2)
+ third parity data (3)
+ first parity data of the does with third parity (1(3))
+ second and third parity data (2,3)
+ first, second and third parity data (1,2,3)
+ all parity data (All)

The pseudo-expectation approach to estimate variance components

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(Schaeffer, 1986) has been applied to every trait-data set combination. This method tries to approximate REML, but is less demanding in computation and is not free of selection bias (Outweltjes *et al*, 1988). The model used was data set dependent. This was the one used for BLUP of line V to analyse data sets involving several parities together, in other cases, L_i (reproductive state of the doe only for first parity data set) and p_k (permanent, nongenetic, effect of the doe on all its parities) were eliminated.

The final output of the pseudo-expectation method is an estimation of the variance components considered and the corresponding fixed effect estimates and random effect predictions (additive or additive and permanent effects).

The variance components estimates were used to estimate heritabilities and repeatabilities. The year-season estimates were regressed on year-season number to estimate the environmental trend, and the average of additive predictions by generation regressed on generation number estimated the genetic trend (Sorensen & Kennedy, 1984).

Results and Discussion

Table III shows the phenotipic means of litter size traits and the higher litter size of V line is noticeable.

TABLE III - PHENOTYPIC MEANS (M) AND STANDARD ERRORS (SE) OF LITTER SIZE AT BIRTH (NB), AT WEANING (NW) AND AT 77 DAYS (NS)

TRAIT	NB		NW		NS	
	M	SE	M	SE	M	SE
PARITY			LINE A			
1st	6.297	(.073)	5.234	(.075)	4.529	(.075)
2nd	7.386	(.102)	5.978	(.100)	5.049	(.098)
3rd	7.142	(.131)	5.887	(.123)	5.1	(.121)
All	6.891	(.050)	5.656	(.048)	4.867	(.048)
			LINE V			
1st	7.891	(.077)	6.807	(.084)	5.684	(.090)
2nd	9.253	(.130)	7.668	(.121)	6.683	(.122)
3rd	9.783	(.135)	8.043	(.120)	7.135	(.126)
All	8.959	(.056)	7.51	(.051)	6.579	(.052)

Table IV gives the estimates of the reproductive state effects. Nulliparous does have a lower litter size than the others, the difference ranging between 0.57 and 1.40. The differences decrease from birth to 77 days. The effect for lactanting does and for non lactanting non nulliparous does is very similar in line A, but is higher for the latter in line V, mainly at weaning and 77 days.

TABLE IV - REPRODUCTIVE STATE EFFECT. NULLIPAROUS EFFECT IS TAKEN AS ZERO, L (LACTATING DOE), NL (NON LACTATING DOE),

LINE	A		V	
TRAIT	L	NL	L	NL
NB	1.13	1.14	1.35	1.40
NW	0.84	0.83	0.66	1.23
NS	0.64	0.69	0.57	1.20

The importance of year-season effects can be appreciated in Table V. It is important to note the high magnitude of these effects, two to four times the values of reproductive state effects. The minimum interval of year season effects is 0.8 standard deviation units and the maximum is close to 2.0.

TABLE V - INTERVAL OF VARIATION OF YEAR.SEASON EFFECTS EXPRESSED IN STANDARD DEVIATION UNITS.

PARITY ORDER / TRAIT	3rd	2nd	1st(3rd)*	1st	2nd,3rd	First three	All
			LINE A				
NB	1.222	1.399	1.463	1.240	0.882	1.030	0.841
NW	1.221	1.102	1.907	1.221	0.898	1.058	0.815
NS	1.649	1.259	1.671	1.660	1.389	1.425	1.256
			LINE V				
NB	1.038	1.070	1.305	1.023	1.147	0.967	0.848
NW	0.945	1.160	1.412	0,946	1.189	0.983	0.931
NS	1.219	1.381	1.072	1.221	1.366	1.203	1.277

* First parity data of does reaching third parity

The estimates of phenotypic variance and repeatabilities are shown in Table VI. The minimun phenotypic variances correspond to first parities in agreement with their lower litter size, and the maximun to the others.. When comparing lines, the maximum phenotypic variances (first parity excepted) are in line V, the line with the highest prolificacy. Repeatabilities range from 0.08 to 0.21 agreeing with other estimates (García *et al*, 1982) in the literature. Generally speaking, values for line V are lower than for line A, and repeatabilities for litter size at weaning and 77 days decrease when parities are analysed together.

TABLA VI - PHENOTIPIC VARIANCE (PV) AND REPEATABILITY (RE) ESTIMATES.

TRAIT	NB		NW		NS	
PARITY ORDER	PV	RE	PV	RE	PV	RE
			LINE A			
1st	6.66		6.86		6.40	
1st(3rd)*	6.50		6.47		6.15	
2nd	7.84		7.58		6.91	
3rd	8.11		6.70		6.57	
2nd,3rd	7.84	0.19	7.23	0.15	6.62	0.19
first three	7.22	0.21	7.01	0.15	6.49	0.16
All	7.20	0.19	6.76	0.13	6.30	0.12
			LINE V			
1st	5.50		6.43		6.87	
1st(3rd)*	5.10		5.31		6.25	
2nd	11.97		10.40		10.07	
3rd	9.98		7.64		7.87	
2nd,3rd	10.85	0.21	9.01	0.16	8.95	0.17
first three	8.59	0.14	7.98	0.10	8.08	0.10
All	9.04	0.17	7.55	0.10	7.61	0.08

* First parity data of does reaching third parity

The estimates of heritabilities are given in Table VIII. It appears that the highest values correspond consistently to first parity and there is a monotonous trend to decreasing values from first to third parity of line V. One explanation of these results is that heritabilities of second and third parities have been underestimated and Table VII presents the cause: the decreasing connectedness between records of close relatives (mother daugther) with increasing parity order. Table II shows that many does fail to achieve a second or a third parity, specially in line A.

TABLA VII - HERITABILITY ESTIMATES OF LITTER SIZE AT BIRTH (NB), AT WEANING (NW) AND AT 77 DAYS (NS)

PARITY ORDER	3rd	2nd	1st(3rd)*	1st	2nd,3rd	First three	All
TRAIT			LINE A				
NB	.011	.030	.069	.104	.034	.076	.066
NW	.049	.051	.022	.099	.087	.085	.077
NS	.045	.072	.026	.123	.061	.084	.074
			LINE V				
NB	.004	.069	.118	.139	.006	.019	.029
NW	.000	.066	.035	.108	.003	.013	.016
NS	.003	.079	.093	.117	.007	.015	.012

* First parity data of does reaching third parity

In order to check this explanation we have carried out the analysis of first parity data of the does which aachieved third parity. The estimates are always lower than the ones obtained for all data of first parity, checking the explanation. However, to have a more complete explanation, it is necessary to admit lower true heritabilities of third parity litter sizes in line V, and for third parity litter size at birth in line A, that the ones for first and second parity.

TABLE VIII - PERCENTAGE OF DOES WITH A GIVEN NUMBER (NAD) OF SUCCESIVE FEMALE ANCESTOR WITH RECORD IN THE PARITY EXPRESSED

LINE	A			V		
PARITY	1st	2nd	3rd	1st	2nd	3rd
NAD						
0	8.3	20.1	35.8	8.5	13.9	23.8
1	11.1	18.4	25.0	10.1	12.0	21.8
2	9.6	15.6	19.4	11.4	13.9	24.8
3	8.8	10.9	11.6	17.8	18.4	14.7
4	7.2	6.3	4.8	16.5	19.7	10.5
5	9.7	6.1	3.9	18.0	14.5	3.0
6	13.0	7.7	0.5	13.4	7.7	1.2
7	10.9	5.7	0.0	4.3	0.0	0.0
8	9.9	4.0	0.0	-	-	-
9	11.5	5.2	0	-	-	-

A second point in Table VII is the consistency of heritability estimates of more than one parity, lower than for first parity. When several parities are analysed together the connectedness between relative records is better than for first parity data. Consequently, the explanation of these results must be necessarily different. It is possible to explain these estimates if different heritabilities and no one genetic correlations between parities are admitted. In accordance with the discussion about third parity estimates, it is necessary, again, to accept very low heritabilities for third parity litter size in line V. All heritability estimates involving third parity in line V are extremely low. The heritability estimates obtained with the model of repeated records of the same trait, when in fact the records have different heritabilities and genetic correlations less than one, are as reduced as the differences in the heritabilities are greater and the genetic correlations lower. Summarising the discussion about heritability estimates we can conclude:

a) First parity litter size heritabilities are 0.1 o higher.
b) Second and third parity litter size heritabilities in line V are lower than for first parity, the heritabilities for third parity being the lowest.
c) Second and third parity litter size heritabilities at birth in line A are lower than the one for first parity.
d) Genetic correlations between litter sizes of different parities are less than one.

Similar results has been obtained in pigs by OLLIVIER & BOLET (1981) and by LE ROY *et al* (1987).

TABLE IX - GENETIC TREND FOR LITTER SIZE AT BIRTH (NB), AT WEANING (NW) AND AT 77 DAYS (NS)

TRAIT	NB		NW		NS	
PARITY	b	SE	b	SE	b	SE
			LINE A			
1st	.045	(.004)	.054	(.003)	.076	(.006)
1st(3rd)	.023	(.001)	.010	).001)	.013	(.001)
2nd	.008	(.002)	.020	(.002)	.036	(.002)
3rd	.004	(.001)	.020	(.003)	.017	(.008)
2nd,3rd	.017	(.003)	.061	(.004)	.049	(.002)
First three	.058	(.005)	.100	(.004)	.111	(.003)
All	.059	(.006)	.102	(.006)	.108	(.005)
			LINE V			
1st	.052	(.012)	.064	(.007)	.072	(.007)
1st(3rd)	.036	(.009)	.018	(.003)	.040	(.008)
2nd	.062	(.009)	.066	(.007)	.070	(.010)
3rd	.000	(.000)	.000	(.000)	.000	(.000)
2nd,3rd	.006	(.001)	.003	(.000)	.007	(.001)
First three	.022	(.003)	.024	(.002)	.024	(.002)
All	.040	(.006)	.033	(.003)	.025	(.003)

b: Regression coefficient of year season effects on year season number
SE: Standard error

Additional support to the conclussions given above can be obtained by looking at the estimates of genetic (Table IX) and environmental (Table X) trends. With generations non overlapping and selection some inadequacies in the model can biass the estimation of genetic and environmental trends (Meyer, 1987). If you underestimate the genetic trend, the environmental trend is correspondingly overestimated. Taking as reference the environmental trend estimated when analysing first parity data, higher values in other cases will express underestimation of the genetic trend. It happens consistenly for all cases, but the most important differences are when the second and third parity data are analysed separately, and when the first three parities or all data are analysed together only the line V shows a relevant difference in environmental trends with respect to first parity. This is in agreement with the higher diversity postulated above for this line in the genetic determinination (heritabilities and genetic correlations) for litter size of different parities. The very high prolificacy of this line, after first parity, close to an eventual limit, is important in understanding the differences found between parities in line V, and the differences between both lines.

These results show a way to increase the efficiency of the selection of litter size. A multivariate approach, considering as different traits litter size of different parities seems to be necessary in some lines, as line V. Nevertheless the task to estimate properly the genetic parameters underlying this model is not an easy one.

TABLE X - ENVIRONMENTAL TREND FOR LITTER SIZE AT BIRTH (NB), AT WEANING (NW) AND AT 77 DAYS (NS)

TRAIT	NB		NW		NS	
PARITY	b	SE	b	SE	b	SE
			LINE A			
1st	-.004	(.016)	.001	(.018)	-.010	(.026)
1st(3rd)	-.010	(.019)	.009	(.021)	.020	(.022)
2nd	.080	(.019)	.062	(.017)	.059	(.022)
3rd	.043	(.024)	.033	(.026)	.047	(.025)
2nd,3rd	.056	(.013)	.043	(.013)	.061	(.017)
First three	.015	(.010)	.008	(.011)	.008	(.015)
All	.022	(.009)	.010	(.009)	.012	(.014)
			LINE V			
1st	.016	(.026)	.039	(.029)	.100	(.035)
1st(3rd)	.066	(.031)	.064	(.038)	.086	(.041)
2nd	.100	(.029)	.106	(.032)	.151	(.034)
3rd	.128	(.023)	.113	(.031)	.186	(.040)
2nd,3rd	.114	(.020)	.113	(.024)	.167	(.027)
First three	.088	(.016)	.082	(.018)	.126	(.022)
All	.077	(.017)	.073	(.018)	.121	(.021)

b: Regression coefficient of year season effects on year season number
SE: Standard error

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